3.—Botany in Western Australia: A survey of progress: 1900-1971

Presidential Address, 1971

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Introduction

In selecting the above topic for this presidential address I have been very mindful of the important part played over the years by the Royal Society of Western Australia. Many of the discoveries and developments in botany in this State have been recorded through the Journal of the Society and several presidential addresses have been concerned directly or indirectly with the plant world.

The aim of this survey is to summarize what has been achieved in botany in Western Aus-tralia specifically relating to studies involving native plants, to try and indicate what imbalances have occurred and to suggest future approaches. The period from the start of the century up to the present time has been selected largely because it was in the early 1900s that facets other than purely descriptive ones in botany first began to be apparent here. To place the whole in perspective it seems desirable, however, to take a brief look at the history of pre-1900 botany in the State. Fortunately much of this has already been well documented. The fascinating story of the work of the early British and Continental botanical explorers has been recorded by Diels (1906), Gardner (1926) and Smith (1958). The human background of the painstaking collecting of native plants carried out by interested early settlers in Western Australia, notably James Drummond and Georgiana Molloy, has been illuminated by the researches of R. Erickson (1969) and A. Hasluck (1965), respectively.

The extent of scientific knowledge of the flora of the State from explorations and collections in the pre-1900 era was made known to the world in certain notable works from which three have been selected for comment. The first two related exclusively to Western Australian flora and the third to that of the whole continent. In his "A Sketch of the Vegetation of the Swan River Colony", Lindley (1839) summarized the then available knowledge regarding the flora. This was derived from a study of an herbarium of about 1000 species comprising the collections mainly of James Drummond and of J. and R. Mangles which had been forwarded to England. Lindley described a large number of new species and listed the synonymies of others in the light of botanical development at that time. The second work dealt with the specimens collected by the German botanist L. Preiss during his stay in Western Australia from 1838-1842. His plant collections were expeditiously worked up and named by a team of outstanding European botanists under the leadership of Lehmann (*Plantae Preissianae* 1844-1848).

The third major work was that of Bentham, and it applied to the whole Continent (Flora Australiensis 1863-1878). This monumental work (which owes much to the co-operation of F. von Mueller in providing specimens and his published and manuscript descriptions of new species) gave an excellent picture of the West Australian flora at the time, although it would now appear that Bentham could have taken greater advantage of the data on the distribution of species documented in Plantae Preissianae (Diels and Pritzel 1904-5; Gardner 1926; Smith 1958), and of Brown's collections at the British Museum (S. Le Moore 1920-22).

Turning now to the history of botany in the post-1900 period, we note the beginning of a wider approach which followed up the visit of the German botanists Diels and Pritzel in 1901-1902. Their first publication, "Fragmenta Phytographiae Australiae occidentalis" (1904-5)was essentially concerned with taxonomy. Many species described new were and they also extended our knowledge of the distributions of known In species. addition their analyses led to the formulation of the boundaries of the botanical districts of south-western Australia which, with relatively minor modifications, have survived to the present day. But it was in "Die Pflanzenwelt von West Australien" (Diels 1906) that the full impact of the then current European botanical thought was felt. Diels applied many of the ideas expressed in Schimper's "Plant Geography upon a Physiological Basis" (published 1898; English edition 1903) to the West Australian scene. He first surveyed the then known plant world of the whole of Australia and used this as a framework for a more detailed account of the western region so as to bring into prominence those vegetative features which give to Western Australia its greatest individuality. He described and discussed the vegetation formations south of the tropic of Capricorn, their ecology (relationship to climate and soil) and distribution, the morphology and anatomy of characteristic plants and the taxonomic relationships and possible lines of evolution of the flora. The impact of these two great works on Western Australian botany appears, however, to have been quite

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limited at the time, due no doubt to their having been published in German. There is no mention of them for instance in the account of the State's flora given by East in "The Cyclopedia of Western Australia (1912). But both works, and particularly that of Diels' have since become veritable source books as taxonomic, ecological and eco-physiological botany developed.

Although botanical exploration and description of new plants by numerous workers proceeded actively over succeeding years, there was a long gap between Diels and Pritzel's books and the appearance of another really significant integrative botanical work. The main reason for this appeared to be that for many years the main thrust of botanical investigation was directed more towards economic aspects, particularly the study of poison plants and of fungal diseases and nutritional problems in crop plants, as increasing areas of land were opened up for agricultural development.

The stage for a more balanced botanical development, however, began to be set in 1926 when Dr. W. Carne (Government Economic Botanist and Plant Pathologist) read a paper at the A.N.Z.A.A.S. meeting in Perth, stressing the need for consolidating the basic floristic knowledge accumulated in the past and advocating the building of a central Herbarium to incorporate collections currently separately housed in the Departments of Forestry and Agriculture² and at the State Museum. He also urged the need for preparation of a Handbook to the Flora, pointing out that Western Australia had fallen far behind the other States in this regard. Following Carne's departure from the State in 1928, his views bore fruit. The position of Government Botanist was in effect recreated, the incumbent of which was to be concerned primarily with flora and vegetation, while the separate position of Government Plant Pathologist was to deal with disorders and diseases particularly in plants of economic importance. One may speculate that the lack of a State Flora long after every other State had such publications, was due partly to the bias towards economic botany from 1910 onwards but perhaps more importantly to the unfortunate fact that successive Government Economic Botanists did

¹ W. Dakin (Professor of Biology in the newly opened University of Western Australia, 1914) quickly appreciated the value of Diel's work and was responsible for a large part of its translation. Owing to his return to England in 1920, however, the work was not completed. A copy of the manuscript, together with some additional translatory notes apparently by Dr. Bennett (Biology Department) and Dr. Herbert (Economic Botanist) was found among early papers in the Botany Department when the writer was appointed here in 1947. Because of its obvious value for teaching and research purposes, the translation was completed. It is currently being updated with a view to its possible publication.

Further note.—A second typed copy of the original translation with additional notes by D. Herbert and C. A. Gardner has recently been sighted in the State Herbarium Library. This was bequethed to the Herbarium following the death of C. A. Gardner in 1970.

² Dr. Sutton (Director of Agriculture) first expressed this view in 1923.

not stay long enough in the State to build up an adequate background of knowledge of the flora. The same was true of University appointed botanists. Between the critical years of 1910 and 1928 seven professional botanists came and went. The Economic Botanists, Drs. Herbert and Carne, for instance left after stays of three and six years respectively. The measure of their potential importance for Western Australia had they stayed longer is apparent from the quality of their later work elsewhere in Australia. In the University Professor Dakin and Dr. Cayzer, despite the distraction of World War I, which commenced shortly after their arrival, began to lay the foundations for a newer approach to the flora. (Cayzer for instance had commenced a Key to the Flora of the Swan Coastal Plain area, while Dakin as well as translating Diels' book was studying the biology of the Albany pitcher plant.) However by 1920 both had left the State to carry on their main life work in other universities.

Be the above as it may, with the appointment of C. A. Gardner as Government Botanist in 1929, the short-term pattern of stay changed. allowing a long, uninterrupted build up of knowledge of the flora. Gardner³, who had already been involved for some years in the study of Western Australian plants, first in the Forestry Department, then in the Department of Agriculture where he became Assistant Botanist under Dr. Carne, was soon to provide an important botanical landmark. This was his publication in 1930 of the "Enumeratio Plantarum Australiae Occidentalis. A Systematic Census of the Plants occurring in Western Australia". This listed all the then known native and introduced species (5578 and 275 respectively) in the State. Even more importantly it provided a bibliography listing the authors, journals and dates of publication of the original papers describing the species, and sorted out many nomenclatural difficulties. Over the next three decades C. Gardner was to describe (mainly through the Journal of the Royal Society of Western Australia) a host of new species and to acquire a unique knowledge of the flora. Much of his accumulated knowledge, particularly in relation to the distribution of plants, was contained in his presidential address to this Society in 1942, the title being "The Vegetation of Western Australia with special reference to the Climate and Soils". It is worth noting here that during the 1930s there had also been remarkable developments in the cognate discipline of Soil Science. Dr. L. Teakle, who had spent several years studying soil patterns in Western Australia, in 1939 summarized his results in his presidential address to this Society. His paper entitled "A

³ Dr. Herbert (verbal communication) tells the story of how he first discovered C. A. Gardner. One weekend in 1919 in the Public Library he came across a young man (then a Bank Clerk) who was laboriously copying out keys from Bentham's "Flora Australiensis" in order to be able to identify plants in the field. Finding that his ambition was to become a botanist, Herbert when unable to have him appointed to his own staff, recommended him successfully for a position as botanical collector in the Forestry Department.

Regional Classification of the Soils of Western Australia" apart from mapping and defining soil zones, led to a better understanding of aspects of plant distribution in the State.

Having now provided a background by outlining the more important historical botanical landmarks in so far as descriptive botany is concerned, we may next turn our attention to examining in detail progress in the different facets of botany. In relation to this survey and assessment of progress it is necessary to appreciate that since 1900 there has been a continuing and accelerating tempo of change in the pattern of botanical interests, in concepts and climate of thought leading to the development of many new branches. Modern botany is in all its ramifications a huge field and partly because of this it is subject to differential development. Professor Bower (1938) in reviewing 60 years of Botany in the United Kingdom, makes an apt analogy to illustrate this development of botanical study as a whole.

He describes it as being similar to the progress of a flock of sheep advancing fan-like over a large plain. The irregularities of formation which develop are defined either by individual enterprise or by the varying richness of the pasture. In a similar way botanists stimulated by individual originality or by opportunity may develop some part too far and too fast; other parts may lag behind unduly as being relatively unfashionable so that individual branches of specialisation may lose touch with one another and an imbalance develops. If this picture be representative of the growth of botany in a major world centre showing that certain imbalances do occur, how much more likely would it be expected to show up and in a more extreme form in a geographically isolated State with so few working botanists. In fact, such imbalances have occurred. Fortunately in our time with the wider representation of different major branches of modern botany active in the University, the State Herbarium, the King's Park Botanic Gardens and the Regional Division of C.S.I.R.O., imbalances if they occur are now less likely to persist. But it is a position that needs constantly to be reviewed. The sub-branches or divisions of modern botany which have relevance for this review are numerous. We may now proceed to examine these to assess wider scientific aspects of botanical achievement in Western Australia.

Classical or Alpha Taxonomy

Over the period of time covered in the preceding largely historical review, taxonomy dealt mainly with the study of classification or the ordering of plants into classes essentially on the basis of their morphology. The fitting of distinct latin names to each of the classes recognized in a classification is referred to as nomenclature. Over the years a "code" of rules governing the application of names to plants had been developed. The basic unit was the "species" which was accepted at the time as having objective reality and some degree of permanence. The methods of description were based on individuals and the "type" concept.

Before proceeding to discuss newer aspects of taxonomy some further comments regarding the status of basic descriptive taxonomy in Western Australia may be made. At the time that Diels and Pritzel came to Western Australia in 1901-1902, the lay opinion was that there was little or nothing more to be learnt about the flora. When, however, Diels and Pritzel's extensive collections were worked up, 55 new species were described and they provided also much new data on distribution and growth forms of earlier described plants. Although over succeeding years many new plants continued to be discovered the lay view persisted that the flora had been thoroughly dealt with. Both Carne and Gardner in the mid-1920s had occasion to deprecate this. A vindication of their view is contained in the fact that since the publication of Gardner's "Enumeratio Plan-Occidentalis" tarum Australiae in 1930. several new genera and at least a hundred new species have been found. Interestingly enough also, the majority of these were found in the better explored south-west botanical province. When the flora north of the Tropic of Capricorn comes to be more intensively collected there will no doubt be a very highly significant increase in the number of taxa. This should dispel any idea that taxonomists spend much of their time working over "old hay". So far, a State Flora has not eventuated.¹ However, now that the State Herbarium is housed in its own specialist building with excellent back-up facilities, its scientific staff can give more time to rescarch and the outlook is hopeful. The publication for instance in the Herbarium's new journal "Nuytsia" of revisions of key genera in the family Rutaceae (Wilson 1970) and the check list of the Orchidaceae (George 1971) are essential steps towards the preparation of a regional flora which might precede and so pave the way for any new "Flora Australiensis".

It seems appropriate here also to refer to the contribution to the knowledge of the southwestern flora by the amateur botanist, Dr. W. Blackall. Exercised by the fact that by the mid-1930s there was still no current handbook available on how to identify flora, Blackall (who had collected extensively on joint expeditions with the Government Botanist) conceived the idea of producing illustrated keys for this purpose. He had made considerable progress with this work but unfortunately he died in 1941 before the project could be completed. As the Government Botanist and his staff, committed as they were to the State Flora, could not complete it, the work lay dormant for several years. Fortunately the Senate of the University of Western Australia on being presented with the manuscript in 1948 was persuaded of its potential value and commissioned the Head of the Botany Department to complete it with a view to publication. The work proceeded and Part I was published by University of W.A. Press (as by Blackall, cdited by Grieve) in 1954, Part II (Blackall and

¹ Part 1. The Gramineae, by C. A. Gardner was published in 1952.

Grieve) in 1956, Part III (Blackall and Grieve) in 1965, while the final volume is nearing completion. The publications by R. Erickson providing descriptions and keys for the identification of Orchids (1951, 1965), Trigger Plants (1958), Droseras (and other insectivorous plants) (1968), constituted another highly valuable approach. Mention must also be made of the publication in 1965 (revised 2nd edition, 1970) of "A Descriptive Catalogue of Western Australian Plants" edited by Dr. J. Beard, Director of King's Park and Botanic Gardens. This provided an up-todate listing of the species housed in the State Herbarium together with notes on their habitat, habit of growth and flowering period.

The above publications helped to make more generally accessible the accumulated floristic knowledge in the State. The corpus of the more recent scientific material which they incorporated was built up by a large number of botanists from the post-Bentham-Mueller era to the present time. These researchers include C. Andrews, L. Diels, K. Domin, A. Ewart, W. Fitzgerald, D. Herbert, K. Krause, J. Mildbraed, S. Le Moore, A. Morrison, C. Ostenfeld, E. Pritzel, A. Purdie and O. Sargent, who were active between 1900 and the early 1920s.1 Over the period 1922-1942 (and to a lesser extent up to 1964) the local taxonomic scene was dominated by C. A. Gardner with his numerous publications, particularly in the Royal Society of N. Burbidge, working in Western Australia. Western Australia, studied and published papers dealing with the Triodia grasses between the years 1938 and 1944 (also up to 1960 from the eastern States after joining C.S.I.R. [now C.S.I.R.O.]). Over a wider period and extending up to the present the contributions of eastern States based botanists and of overseas botanists studying pan-Australian genera are notable. Prominent among these are C. Ali, A. Barlow, R. Belcher, S. Blake, J. Black, B. Briggs, G. Benl, H. van Bruggen, N. Burbidge, R. Carolin, G. Davis, H. Eichler, E. Ising, L. Johnson, F. Kraenzlin, N. Lothian, R. Melville, C. Norman, C. Rao, A. Orchard, H. Rupp, R. Schodde, A. Schindler, V. Summerhayes, D. Symon, M. Tindale, J. Vickery, L. Watson, J. Willis, and E. Wimmer. The decade 1960-1970 was marked by a significant number of taxonomic publications appearing from members of the staff of the State Herbarium (R. D. Royce, P. Wilson and A. George), from G. Smith (University) and co-workers, from Dr. N. Brittan (University) and his research students and from a visiting botanist from U.S.A., S. Carlquist.

In all, the above adds up to an impressive amount of progress in descriptive taxonomy. From current observations it is apparent that the discovery and description of new species is continuing at an active rate, while the review and redefining of older ones is receiving increasing attention. The stronger emphasis on monographic studies of families and genera is also an encouraging trend.

Experimental Taxonomy or Biosystematics

The last 30-40 years has seen the rise of what has been called Experimental Taxonomy which co-exists with and overlaps descriptive Taxonomy. The term Biosystematics is also used and this perhaps indicates more clearly the emphasis which is placed on the application of cytogenetic, biochemic, morphologic, anatomic and statistic procedures on the identification of evolutionary units, the use of experiment to determine their genetic inter-relationship and the part the environment plays in their formation. By its nature this work involves considerable use of laboratory techniques and its development in this State so far has consequently been closely associated with the Botany Department in the University of Western Australia with its specialist in this field (Dr. N. H. Brittan) and his higher degree students. Some of these latter one may note belong to the State Herbarium staff so that these newer approaches may be expected to develop further there. Dr. Brittan concentrated on the variation, classification and evolution of flowering plants with particular reference to the genus *Thysanotus* in the Liliaceae. His study of this genus has provided evidence of variation at single gene mutation level (flower colour) and of polyploidy. This topic provided the subject for his presidential address to the Royal Society of Western Australia in 1962. In addition, his comparative anatomical and other investigations of Thy-sanotus species have proved very helpful in Descriptive Taxonomy (1960, 1971). Three of Dr. Brittan's research students have also made definitive contributions. J. Green (1960) examined the Haemodoraceous genus Conostylis and studied its inter-generic relationships with Blancoa, Anigozanthos, Macropidia and Tribonanthes. It is of interest to note that recently a Netherlands botanist, Geerinck (1969) has implemented a change foreshadowed by Green involving the suppression of the genus Blancoa, placing the single species under Conostylis. E. Bennett (nee Scrymgeour) (1970) has studied the taxonomy and cyto-taxonomy of all the Australian species of Hybanthus and the work has led to the erection of a new species. Ten Choo (1970) dealt with the genus Lomandra in the Xanthorrhoeaceae, and showed that anatomical features of the leaf were helpful as a supplementary basis for classification. Study of the variation in the inflorescence led to the postulation of possible lines of evolutionary development.

The above researches on experimental taxonomy have allowed a clearer understanding of the limits of the genera so far studied and have as well clarified many points at the species level. It is hoped that this newer experimental approach will intensify in the future.

Plant Geography

Knowledge of the distribution of plants is naturally closely related to taxonomy but it is also part of the study of regional communities and merges into ecology. In its wider aspects

¹ For	a	complete	list	see	С.	Α.	Gardner,	(1926)	under
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the plant geography of Western Australia can not be considered independently of that of the whole of Australia, while the Continent itself has to be fitted into the overall scheme of world plant geography. Our appreciation of plant distribution is affected by our knowledge of the changing distribution and extent of land masses and oceans throughout geological time and by theories such as Continental Drift. The words of Shakespeare's Henry IV apply very aptly for Australia:

"Oh God! that one might read the book of fate,

And see the revolution of the times

Make mountains level, and the continent,

Weary of solid firmness, melt itself into the sea!"

Western Australia owes much of its vegetative uniqueness to just such a sea encroachment The first post-1900 study involving Western Australia was by Diels (1906). He applied many of the new Schimperian concepts in discussing our vegetation scene and for a long time this account stood as the only analysis of plant distribution here, and of the State's floristic relationships with other parts of Australia. Gardner (1926, 1942) re-examined the plant geographical situation in the light of the additional evidence available to him from exploration and collection, and elaborated on Diels' analysis. It was not until 1947, however, that a further big advance came when Crocker and Wood in South Australia presented their findings arising out of the greater knowledge becoming available of the climatic and soil patterns of Australia and of the post-Tertiary historical sequences. They ascribed the high degree of endemism in south-west Australia to the fact that it had been effectively isolated by inundation of a large part of southern Australia in the Miocene. Then despite the retreat of the sea during the later Pliocene period the isolation of the flora had been maintained by edaphic factors (calcareous soils) and by climatic factors. The presence of lateritic soil in the south-west of Western Australia was considered to be the factor largely responsible for the selection of the Australian element there.

Burbidge (1960) in a re-examination of the phytogeography of the Australian region accepted the concept that floristically southwestern Australia had been isolated by both geographic and climatic factors. She noted also that it was far from any well-marked migration route and lacked special affinities with South African flora, although this might have been expected under the Continental Drift hypothesis. She considered that it was because of the relative difficulty of communication with the tropical zone and with some other parts of the temperate zone, that a highly endemic flora had developed. These factors were also responsible for the persistence of many relicts. Burbidge emphasized the strong generic affinities with the South American flora strengthening the view that in the past there had been communication between the two land masses. In this connection the

discovery of the Rafflesiaceous parasitic plant *Pilostyles hamiltonii* (Gardner 1948) in the southwestern botanical province has great significance.

Reference may also be made at this point to the valuable palaeobotanical work of Churchill (see pp. 40-41) in relation to the Plant Geography of Western Australia. J. Green (1964) presented details of distribution of discontinuous and presumed vicarious species pairs in southwcstern and south-eastern Australia. Selected species are discussed in relation to the geological and climatic history of Australia. He considered that while the discontinuity for most of the species could be explained on the basis of Crocker and Wood's or Burbidge's hypotheses the possibility that some disjunctions may have their explanation in long-distance wind dispersal should not be ruled out. In connection with the above problem of discontinuous distribution the work of Anway (1969) and of J. A. McComb (1966) in the Cytogenetics and Genetics section (pages 43-44) should be consulted.

One of the important features of the Western Australian flora is its high degree of endemism. Gardner (1959) and Royce (1965) have pointed out that the endemism is especially noticeable in the south-western vegetation province and they have estimated it to be as high as 75 per cent. The most recent study of endemism at the species level has been carried out by Beard (1969). He analysed data for the three Western Australian vegetation provinces and found the values to be as follows:- South-western 79 per cent, Northern 77 per cent and Eremean 45 per cent. With regard to the plant geography of the Northern province, Gardner (1942, 1959) described the salient features indicating the importance of the Indo-Melanesian (Palaeotropic) and Madagascan elements in relation to the dominant Australian element in the flora. Beard (1967) in connection with his study of northern vegetation types, has provided the most recent comment. It seems clear that much more collecting work needs to be done and data on taxa and distribution patterns built up to allow more meaningful conclusions to be made regarding the overall plant geography of the Northern province.

Ecology

Plant ecological studies have gone through a series of phases from the early descriptive investigations where habitat and soil relations of vegetation were examined, through the successional, the edaphic and eco-system approaches, becoming increasingly quantitative and sophisticated. Some of these phases are represented in larger or smaller degree in ecological research in Western Australia and will now be considered. The first descriptive eco-plant geographical study of the south-west and adjacent eremean areas we owe to Diels (1906), who outlined and named the main plant communities, discussed adapta-

tions of plant groups, and in the light of the then available knowledge of climate and soil assessed their relation to the environment.¹ A closer delineation of the forest formations in south-west Australia was made by Gardner (1923-1927), by Kessel and Stoate (1936), and by Brockway (1941). Gardner (1923, 1925) also provided an account of the forest formations of the north-west region.

In the 1930-1942 period, with one important exception (Williams 1932) and apart from Gardner's generalized descriptive account of all the vegetation provinces in Western Australia (1942), no ecological studies in depth were carried out here such as characterized this period in the eastern States. There the earlier accepted views on the relationship between vegetation and its habitat were questioned and tested. Ecological aspects of successsion, of climate, and edaphic climaxes, the nature of associations, consociations, societies and forest types were debated, and considerable increases in knowledge of Australian plant coology and modifications of earlier accepted theory developed (Wood 1939; Pidgeon 1942). The exception mentioned above to the general missing out of this phase in Western Australia was however an important one, and one which if circumstances had favoured its continuation and extension might well have anticipated by several years the break-through on the edaphic climax association made by Wood in South Australia. The work was a small-scale analytic approach with emphasis on the edaphic factor carried out by Williams (Botany Department, University of Western Australia, and under the direction of Dr. Armstrong) in the Darling Range and was supplemented by a further study commenced in the Beraking area. Williams' investigations appear to have been catalysed by the work of the soil scientist, Prescott, in South Australia, who in 1931 had produced the first soil map of Australia and had recognized that the extensive lateritic formations in Western Australia were a fossil soil representing the remains of an ancient B horizon. In his study of the composition of the vegetation in the valleys and on the hill tops in the Darling Scarp area at Darlington, Williams formulated the view that the Eucalyptus marginata association was adapted for laterite and lateritic gravel and that as the plateau became dissected by water courses and as valley formation continued, the E. marginata association was being locally destroyed and replaced by an E. calophylla-E. redunca association. Work on the related Beraking area had also been commenced by Williams in 1932 but

¹ In the wider sense as affecting overall Australian forest ecology, it is of interest to note that, as recently claimed by Specht (1970), an early misinterpretation of the application of Diels' expression "Sclerophyllen-Wald" to the forest tree stratum rather than to the lower storey vegetation and the consequent introduction of derivative terms such as "dry sclerophyll" and "wet sclerophyll" in describing southern and south-castern Australian forest vegetation, has caused much confusion. To overcome this Specht has proposed the term "Shrubby open-forest" for Diels' "Sclerophyllen-Wald".

was interrupted due to his transfer interstate on joining C.S.I.R. (now C.S.I.R.O.) later that year. The field work for the Beraking study was completed when he came back later on a brief visit to Western Australia and the paper was communicated to the Royal Society of Western Australia in 1944 but due to the war was not published until 1948. The conclusions he reached were that the distribution of plant communities could be determined by edaphic factors such as soil type (determined by the underlying rock formations), the maturity of such soils and the soil water relations, as Wood (1939) had by then thoroughly worked out in South Australia. Williams in his paper points up an imbalance. commenting rather sadly on how Western Australia had lagged far behind the other States in these aspects of the study of ecology.

It is appropriate also to note here a further development in the soil science field in Western Australia which had an impact on ecological aspects of vegetation study. Trakle (1938), building on the foundations laid by Prescott (1931), described nine main soil zones and thirty-three regions into which the State could be divided. He showed that the known vegetation types were related to the soil zones and regions and both were closely related to the climatic rainfall factor. Teakle's work was followed by that of Gardner (1942-44) who summarized existing knowledge of the overall vegetation formations of Western Australia and discussed their relationship to climate and soil. During the 1940s also several helpful descriptive ecological accounts were given by Burbidge of vegetation in the north-eastern goldfields area (1941-42), the De Grey-Coongan area $(1942-45)^2$ and the Eighty-Mile Beach $(1941-44)^2$ before she too left the State on joining C.S.I.R. From about 1950 onwards more attention was focused on ecological work by the University Botany Department and a series of studies were made by different research students under the direction of B. J. Grieve and A. M. Baird. A. Holland (M.Sc. Thesis 1953) studied the ecology of *Eucalyptus* formations in the south-west and southern eremean regions. He found the edaphic factor to be dominant over the climatic factor in maintaining associations and suggested that the vegetation was possibly selective with respect to micro-nutrient elements, since N and P were low in all vegetation zones examined, and pH was not a factor. In commenting upon the existence of outliers of E. marginata (near Kulin) and of E. diversicolor (at Porongurups and Mt. Manypeaks), and on the occurrence of fossil podsols and of wave platforms cut in the shore line, Holland suggested that climatic fluctuations had taken place with a warm wet period occurring possibly between 4000 to 8000 years ago. It may be interpolated here that D. Churchill (Ph.d. Thesis 1961, published in part 1967), using a palaeoecological approach provided confirmatory evidence indicating that climatic fluctuations had affected distribution of E. diversicolor and E.

² Publication delays due to the war.

calophylla. The climate appeared to have been wetter from 4 000-3 000 B.C. and then gradually became drier, with further fluctuations between wet and dry up to the present time.

N. Speck (M.Sc. Thesis 1952) dealt with the ecology of the metropolitan sector of the Swan Coastal Plain. He recognized two formations, dry sclerophyll forest and scrub. E. gomphocephala (tuart) was found essentially only on the Cottesloe Soil Association, while E. marginata occurred on the yellow sands of the Karrakatta Soil Association, the deeper sands of the Cottesloe Association and the gravelly sands of the Forrestfield Association. Other plant associations, consociations and their faciations were also shown to be closely associated with particular soil types. Climate, notably rainfall, was found to affect distribution, while bush fires were recognized as the most important biotic factor operating. Speck's work also included an ecological study of the University Botany Department reserve at Cannington. This area, subject to flooding in winter and severe dryness in summer, provided an ecological niche for many unusual plants which now appear to be at risk due to changes in drainage arising out of increasing urbanisation. The vegetation of the Darling and Irwin botanical districts was also studied by N. Speck (1958) who concluded that while climate was the over-riding factor in the selection of vegetation of the area as a whole, the edaphic factor determined the distribution of communities within the area. He confirmed that the 17.5 cm winter rainfall isohyet, as indicated by Gardner (1942) more clearly defined the limits of the south-west floral elements than the original 30 cm line (average yearly rainfall) of Diels and Pritzel (1904-5). Speck also modified Diels and Pritzel's out-line of the Avon botanical district, separating the more northerly part to form a new district which he called Lesueur. The line of separation was clearly marked by a change in soil typ γ . Dr. Brittan, with his research student Silskury (1955), in studying the ecology of Kennedia, showed that within a single climatic zone the edaphic factor (podsolic or lateritic soils of inherently low fertility) was the most important. The vegetation and soils of Garden and Carnac Islands were described by W. McArthur (M.Sc. Thesis 1952, published 1957). Following a disastrous fire on Garden Island in 1956, the process of regeneration of the Acacia, Callitris and Melaleuca communities was studied by A. M. Baird (University, Botany Department staff), the work being published in 1953.

It may be noted here also that Miss Baird has for several years been making a study of the effect of fire on regeneration of native species on the mainland with special reference to the Swan Plain area and specific plots in King's Park. It is anticipated that findings from this work will be published in due course. Regarding the effect of fires on vegetation, Gardner (1959) noted the fact that some plant communities included a number of species which were apparently well adapted to periodic fires.

The vegetation patterns on other islands off the south-west and southern coasts have been recorded by a number of workers as follows:-Rottnest Island, Storr, Green and Churchill (1959); Abrolhos Islands, Storr (1960, 1965); Bernier and Dorre Islands, Shark Bay, Royce (1962); Recherche Archipelago, Willis (1953). Descriptive accounts of the ecology of various arcas in the lower south-west have also been made. G. Smith (University Botany Department staff) dealt with the vegetation of the Poron-gurups (1952), while J. S. Beard (King's Park Botanic Gardens) noted relationships between "stripe" patterns in plant communities and soil conditions in the Ravensthorpe area. The work of Holland (1953) in this area has already been mentioned. Lange (1960), in an autecological study of the relationship of twelve tree species in an area of transition near Narrogin, found that the incidence of the species related to soil surfaces and to rainfall.

Sand dune vegetation in the region approximately 20 miles north and south of Perth has been studied by G. Smith (1957, 1970), while Sauer (1965) has surveyed the seashore vegetation over more extensive northern coastal areas.

The study of "wetland" ecology has attracted relatively little attention so far despite the fact that such studies are clearly becoming urgent. A valuable pioneering study in depth has however been made by Drs. J. A. and A. J. McComb (University Botany Department) dealing with the Loch McNess fresh water lake area in Yanchep National Park (1967). They recognized sedge swamp and sedge fen and showed that these were similar floristically and structurally to those found in wetlands elsewhere in Australia and abroad.

Turning now to more northern botanical areas we may note the descriptive accounts of W. Fitzgerald (1916) and Gardner (1923, 1925, 1942). Gardner and Bennetts (1956) delineated more precisely in map form the boundaries of the botanical districts north of the Tropic of Capricorn. Burbidge, in addition to her earlier mentioned descriptive ecological studies in the north-west, also published on the Pilbara area (1959), and described the ecological succession after fire in Triodia grasses (1943), while Royce (1964) discussed the relation of soil and climatic conditions on Depuch Island near Roebourne. More detailed coological accounts of the vegetation of the North Kimberley and West Kimberley regions and of the Meekatharra-Wiluna area have been given by the C.S.I.R.O. botanists Perry (1970), Speck (1958, 1960, 1963), and Speck and Lazarides (1964).

With regard to inland desert areas we may note first the work of E. R. Johnson and A. M. Baird (1970) who gave an account of the flora and vegetation of the Nullarbor Plain near Forrest, and of J. Willis who described vegetation in the Eucla district (1959). Dr. J. S. Beard (1968, 1969) has made a special study of the ecology of desert regions, namely:—the Great Sandy Desert, the Gibson Desert, the Great Victoria Desert and the Nullarbor Plain. These

comprise about two-fifths of Western Australia, He subdivided these desert areas into botanical districts or natural regions each of which has its own characteristic landscape and vegetation. The principal vegetation types present are Triodia hummock grassland, Mulga scrub (on red loams) and Mulga parkland (on laterite), Tn a further development of his ecological studies Beard is currently systematically describing and mapping the vegetation of Western Australia (1969a, 1971). In addition the first of a series of vegetation maps in colour together with an explanatory memoir (commenced while Dr. Beard was Director of King's Park and Botanical Gardens and continued in association with Professor Webb, Geography Department, University) is being prepared for publication. The extension of this approach has great importance for our knowledge of the overall ecology of the State.

Finally mention must also be made here of the work done by a State Sub-Committee (under the chairmanship of Dr. Ride, Director of the Museum, and appointed by the Australian Acad⁻my of Science) in listing details of all National Parks and Nature Reserves throughout the State (1963). This compilation is of great value for future vegetation studies as well as recording the present degree of conservation of State flora and fauna areas,

Statistical Ecology

The use of statistics in the analysis of distribution of individual species within communities and in relation to the classification of plant species began to find application in Europe and the United States of America during the early 1930s. In the post-war period this approach intensified and methods were rapidly developed whereby vegetation could be described quantitatively. Such descriptions could then be used as a basis for classification or ordination. Dr. Goodall (while with C.S.I.R.O. in Perth and Hon. Reader in Botany in the University of Western Australia) published many papers in this field (1963, 1964, 1966, 1967). Although most of these were theoretical in approach and so applied to statistical studies of vegetation in general, we may note that part of the data on which they were based had been obtained in the course of his study of Western Australian vegetation. One of Dr. Goodall's research students in the University (W. A. Loneragan) is currently applying selected statistical procedures in a study of portions of the Jarrah forest and across the ecotonal region to the Wandoo woodlands (1966), J, Havel (W.A, State Forestry Department) has also used the objective statistical approach method to analyse and assess through the native vegetation the potential of the northern part of the Swan Coastal Plain for the growth of Pinus pinaster (1968). The production of a computer map of the flora of Western Australia is now highly desirable. In this connection it may be noted that Dr. Goodall has made surveys and samplings of vegetation through a selected region of Western Australia with a view to cominencing the production of such a computer map.

Barrow Island, off the north-west coast, has already been so mapped. Unfortunately this work has been interrupted by Dr. Goodall's departure to take up a Chair of Ecology in the United States of America, but it is hoped that the project may be resumed at some later date.

Palaeobotany, Palynology and Palaeoecology

In discussing the origin of the present Australian flora, Herbert in 1950, could still only conjecture that in the early Tertiary there must have been something like a pan-Australian flora from east to west and so it would have been possible for Beech (Nothofagus) forests to extend to Western Australia where now they could not exist. He makes the comment "The fossil record is however silent on this point". By 1954, Dr. Cookson, a palaeobotanist in Melbourne was able to break this "silence". Already familiar with the micro-flora from the older Tertiary coal seams in Victoria and South Australia, she was able to find matching forms in material sent to her from a carbonaceous deposit obtained from a bore in the Nornalup Inlet area on the south coast of Western Australia. Thus she provided strong evidence that during the early part of the Tertiary (Eocene), the floras of the eastern and western portions of Australia were essentially similar. The scene now changes back to Western Australia where D. Churchill (a Ph.D. student in Botany) had developed a new method for concentrating pollen grains (1957) which facilitated the study (carried out in collaboration with Dr. Balme of the University Geology Department) of pollen grains in carbonaceous sediments at Coolgardie. Pollen grains of Beech (Nothofagus) and pollen of proteaceous and podocarpaceous affinities were identified (1959). Also at this time McWhae et al. (1958) had found Nothofagus, Araucaria, Banksia and Gleichenia in Tertiary (Eocene) sediments near Kojonup. Thus Cookson's discovery was confirmed and extended. Balme and Churchill were also able to suggest that in Eccene times the sea when at its most transgressive phase, must have reached as far north as Coolgardie,

Churchill (1959) next applied his pollen analysis technique to a study of a bore sample of submerged freshwater peat from 68 feet below sea level at the site of the "Narrows" bridge over the Swan River. He was able to show that pollen of Eucalyptus wandoo and E. gomphocephala (Tuart) together with pollen of Casuarina, Acacia and other genera were present. Radio-carbon dating of the peat gave an age of \pm 7900 years B.C. The results indicated that at that time the bed of the Swan River was more than 68 feet below its present level and that clay soils supporting Wandoo and nearby calcareous soils supporting Tuart were present along the river banks. An interesting point made by Churchill was that when the sea was at this low level, Rottnest, Carnac and Garden Islands would have been connected forming high ridges on a coastal plain extending out from the mainland. He believed that the

separation of Rottnest from the mainland must have occurred between 4000 and 5000 years B.C. It is also of interest that Churchill, from his studies on fossil wood from Rottnest Island, showed that *Xanthorrhoea* (Blackboy) which had not been found on the island since white settlement began, was at least represented there before the separation of the island.

In his major thesis study Churchill (Thesis 1961, published in part 1967) used pollen analysis to investigate the prehistoric past of three *Eucalyptus* species (namely *E. marginata*, *E.* calophylla and E. diversicolor) growing near the south-west coast. Fossil pollen was examined from a variety of areas but particularly from the Boggy Lake area near Walpole. Past changes in the relative eucalypt pollen frequencies were dated by radiocarbon assay and were found to cluster around certain dates. Keeping in mind the moisture requirements of the trees (a wetter climate for instance favouring a high E. diversicolor/E. calophylla ratio and vice versa), it became highly probable that the climate was responsible for the long-term changes in pollen frequencies. It was inferred from the strong occurrence of E. diversicolor from at least 4 000 B.C. to 3 000 B.C. that the climate was favourable to this species, and so wetter than at present. Thereafter the ratios suggested that fluctuations in climate occurred up to 1500 A.D. from which time climate has remained more or less as at present. These studies support Holland's conclusions (see page 38) which were reached on other grounds. They also support those of Lange (1960) who in discussing the disjunct distribution of certain tree species in the south-west area considered that increasing aridity was important. He suggested that the species studied had continuous distributions over the area under the rainfall and soil conditions preceding the most recent aridity. The conclusions from the work by Churchill discussed above have wider significance in relation to plant geography and eco-physiology. It is relevant also to note here that Churchill's fossil pollen analyses indicated, in contrast to the views of Pryor and Boden (1962) in eastern Australia, that Eucalyptus pollen was dispersed by wind as well as by insects. It agrees with the work of N. Speck, who noted in a survey of monthly incidence of pollen in the Perth area (1953) that Eucalyptus species contributed 9 per cent of the atmospheric pollen. From the above it is clear that palaeobotany, palynology and palaeoecology have made significant contributions to the understanding of the Western Australian vegetation scene, and emphasizes the advantages of interdisciplinary studies.

Algology

In 1854 the algologist W. Harvey visited Western Australia and made extensive collections around the south-western and southern coasts. The published results (1854, 1858-1863) constitute the basic reference points for algal taxonomy. There was a long interval before fresh floristic and ecological studies of algae were made. These were commenced by G. G. Smith of the University Botany Department staff. His work (M.Sc. Thesis 1951) involved a study of the algal ecology of the Cockburn Sound and Rottnest Island regions, and resulted in the classification of the marine plant communities into twelve plant associations arranged in two formations. Analysis of the causal factors controlling algal distribution suggested that reef terraces played an important part. In further researches, Smith (1956) has described the ecology of Siphonales occurring near Perth and in Hodgkin, Marsh and Smith (1959) has given an account of the algae present around Rottnest Island. In "Seaweeds of our Coast" (Smith 1964) he has also given a general account of marine plant life around the south-west and southern coasts. Two of G. Smith's research students, B. Allender (M.Sc. Thesis 1971) and S. Koh (M.Sc. Thesis 1971) have carried algal ecological studies in Western Australia further. Following up observations by Royce (1955). Allender investigated the macroscopic benthic marine flora of the Swan River estuary, describing the major plant communities of the sand, mud and rock formations. The increasing salinity and higher temperatures of spring and summer were found to be responsible for the occasional "bloom" conditions in some species which caused minor pollution of estuary beaches. Koh made a taxonomic and ecologic study of the *Dictyotalcs* group comprising ten genera and twenty-five species growing along the south-west coast. Five new species were described, while culturing studies showed that in some genera no sexual plants but only diploid (tetrasporic) plants were present. In other genera both sexual and tetrasporic plants were present but the latter predominated. Marine life studies are being extended to include the study of the sea grasses (Posidonia and Amphibolis) by another of G. Smith's students (M. Cambridge). Posidonia *australis* is of particular importance in the ecology of the Cockburn Sound area.

Apart from the above taxonomic and ecologic studies on marine algae it is relevant here to mention certain other developments concerning them which have arisen out of the overall growth hormone studies initiated in plant physiology by Dr. A. J. McComb. With one of his research students (R. Jennings) he found gibberellins to be present in the red alga (Hypnea) growing in the Swan estuary and on ocean beaches near Perth (1967). Further work by Jennings (see under Plant Physiology, page 47) led him to suggest that growth regulating substances may have arisen early in algal evolution. Jennings (1967) also provided an interesting addition to our knowledge of the life history of Ecklonia radiata (the only representative of the Laminariales found in Western Australian waters). He succeeded in growing the gametophyte and the young sporophyte under controlled conditions and showed that both male and female gametophytes were very reduced with most female plants having no vegetative filaments.

There is considerable need for further studies of marine algae to extend our knowledge of their distribution, life histories and overall ecology. In this connection the work of Womersley in South Australia who has included in his study the Western Australian representatives of *Cystophora* present along the south coast (1964), may be noted.

Mycology

The economic importance of fungi as disease agents in crop plants was early recognized in the State by the appointment of a mycologist, and many important studies were made. It is outside the scope of this survey, however, to consider the plant pathological work which has been done in relation to crops, fruit trees and other introduced plants of economic importance. But fungal organisms have also been found which attack native plants and studies on these may be considered here. A list of diseases recorded on native plants was first compiled by W. Carne (1925, 1927) and later revised by Macnish (1963). The list is extensive, 42 genera and 70 species being known to be subject to attack. Where the native plant is of horticultural importance investigations have been extensive. In the early 1930s a canker disease was found to be attacking *Eucalyptus ficifolia*, the Red Flowering Gum. This tree, which in its natural state is confined to a small area on the south coast, had become widely planted in Perth as an ornamental tree. The fungus causing the canker was isolated and described by the Government Plant Pathologist, H. Pittman, in 1935, being named Sporotrichum destructor.

W. Cass-Smith, who succeeded H. Pittman as Plant Pathologist, continued the study and found that the canker disease in a milder form was naturally present on *Eucalyptus calophylla* which was common on the Swan Plain and metropolitan area, and that this had served as the source of infection for *E. ficifolia*. Despite continued study up to the present time no effective chemical or genetic means of control of the disease on the valuable Red Flowering Gum has been found (Cass-Smith 1970).

Another investigation dealing with fungal decay in a eucalypt, E. marginata (Jarrah), was carried out by N. Tamblyn in the University Botany Department. He described five rot conditions and two abnormalities occurring in jarrah as a result of fungal attack (1937). Owing to the lack of any means, at the time, of determining the specific identity of the attacking fungi, the work remained incomplete. It is only in quite recent times that the problem has been taken up again in the Botany Department, and some success achieved in developing identificatory methods for dealing taxonomically with wood-attacking gill fungi, Mr. R. N. Hilton (Botany Department staff) and his research student (H. C. Broughton) are now combining the study of the microscopic features of the sporophores of genera in the families Pleurotaceae and Polyporaceae with microscopic and macroscopic features of pure cultures, to give full characterisation (H. C. Broughton, M.Sc. student 1966).

In another economically serious pathologic condition in *E. marginata* known as "dieback", a break-through has fairly recently been made by Commonwealth and State workers. This involved the isolation of the fungus *Phytophthora cinnamomi* and proof of its pathogenicity by Podger, Doepel and Zentmeyer (1965). The study of basic aspects of the biology of the fungus and of the forest microflora, which is essential in order to develop a method of control of the disease, is proceeding actively at the present time, both at the Commonwealth Forestry Research Laboratories at Kelmscott and at the University Botany Department under a State Forestry Department research fellowship.

A severe disease of native Acacia plants caused by gall-rust (Uromycladium tepperianum) formed the subject of study by J. Goodwin (M.Sc. Thesis 1966). She recorded 60 Acacia species which were susceptible to infection and 118 host species (previously the number of these known was 58). She also increased our knowledge of the life history of the fungus causing the gall formation.

In the course of studies of the pathogen Sclerotinia sclerotiorum another research student (R. Henderson 1962) added considerably to our knowledge of parts of the life history of this fungus.

In other areas of Mycology, research students directed by E. R. L. Johnson and R. N. Hilton have made interesting descriptive and experimental studies. Thus L. H. Tai (M.Sc. Thesis 1964) showed that species of *Saprolegnia* could be infected by the fungus *Olpidiopsis saprolegniae*, being particularly susceptible during their vegetative phase. It was found that nitrogenous materials and xylose as a carbon source tended to increase the resistance of the hosts.

H. K. Tan (M.Sc. Thesis 1966) made a study of the fascinating adaptations which facilitate the trapping of nematodes by a particular group of fungi. He isolated and described 32 species of these nematophagous fungi from Western Australia, three of which were new to science. C. S. Fang (M.Sc. Thesis 1968) extended the scope of earlier work dealing with air-borne pollen (see Speck 1953) by making a detailed study of the diurnal and seasonal changes in the concentration of fungal spores in the air in the vicinity of Perth. Basidiosporcs were found to be the major wet-air spore type in the air around Perth and two hitherto unrecorded groups of these were registered,

The systematic study and naming of field and forest fungi characterized by the presence of macro-fruiting bodies has lagged behind the specific studies on largely parasitic fungi described above. This has been at least partly due to the difficulty of collection and preservation of suitable diagnostic material. E. R. L. Johnson (Botany Department) commenced a mycological herbarium in 1964 and began the process of precise identification. Under the guidance of her successor (R. N. Hilton) the collection is being actively augmented. The preservation of speci-

mens has been facilitated by the application of a new freeze-drying technique. Further study should allow the compilation of a definitive census within the next few years.

With regard to Lichens it may be noted that a definitive list of those known to occur in Western Australia was compiled by P. Bibby and G. Smith (1954).

Plant Anatomy

L. Diels (1906) in "Die Pflanzenwelt von West Australien" touched upon and illustrated the leaf and stem anatomy of certain native plants which showed xeromorphic modifications such as thick cuticles and sunken stomata. Shelton (1921, 1934) also illustrated leaf sections showing these modifications. The first really detailed study of a Western Australian plant, however, was carried out by the Economic Botanist, D. Herbert (1919). This dealt with the leaf, stem and root structure of Nuytsia floribunda. It arose out of the discovery that the fine rootlets of this tree were parasitizing roots of other plants. As well as showing the nature of the parasitism the anatomic work explained certain other strange features in Nuytsia such as the habit of stem growth and the unusual brittleness of the branches. These were shown to be related to the unusual and remarkable method of secondary growth of the tree. No further histological studies in depth of Western Australian plants were made until Burbidge (1946) described the foliar anatomy of members of the grass genus Triodia. She described the way in which the leaf traces passed between the sheath and the nodes, the arrangement of bundles within the sheath, the differential distribution of stomata in grooves in different species and the mechanism of the closing of the grooves on both sides of the lamina during periods of water shortage. The collated information incidentally enabled Burbidge (1946a) to recommend that the name Triodia R.Br. be confined in use to Australian species.

A further long interval occurred before Dr. N. H. Brittan and his research students commenced a series of anatomical studies which were necessary for the elucidation of certain biosystematic problems. Dr. Brittan in the course of his study of 27 species of *Thysanotus* established a correlation between anatomical characters and morphological groupings (1970). J. Green made a study of the anatomy of *Conostylis* species which helped him to develop an identificatory key (1959), while two other research students demonstrated the value of the anatomical approach as an aid to separation of species in *Hybanthus* (Bennett 1970) and in *Lomandra* (Choo 1976).

Using the techniques of both standard and scanning electron microscopy, Dr. Brittan is currently continuing his anatomic studies of *Thysanotus* species. Dr. A. J. McComb and his student C. H. Wong have also employed the electron microscope in their study of cell structure in *Callitriche* (see under Plant Physiology). Mention may also be made of anatomical studies carried out by overseas or eastern States botanists using preserved material collected in Western Australia. Thus C. Wilson (visiting Professor from U.S.A.) studied the floral anatomy of several local species of *Hibbertia* to assist him in enumerating, on the basis of structural features, the probable characters of the archetype of this genus (1965), while S. and D. Carr studied species of Western Australian eucalypts in their investigation of glands and ducts (1969).

Many of the anatomic studies undertaken within the State so far appear to have been designed to help in the elucidation of problems arising out of investigations in cognate branches of botany. While this is of course often necessary and desirable there still appears scope for more thorough-going anatomical studies in their own right dealing with characteristic genera and species, particularly those that are endemic to Western Australia.

Life Histories and Embryology.

Up to 1930 little was known of the details of the life histories of native plants. About this time Miss A. M. Baird (Botany Department staff), having observed the interesting work of Buchholtz in the U.S.A., commenced a study of the embryology of gymnosperms native to Western Australia. The first investigation dealt with Actinostrobus (1937) where she showed that cleavage polyembryony was a constant feature and that distinctive differences from the embryology of other genera in the Cupressaceae were recognizable. The second investigation dealt with Macrozamia riedlei where a new type of polyembryony together with unusual features of pollen formation were reported, enabling her to classify Macrozamia riedlei as one of the more primitive Cycads (1938).

The life histories of several species of *Callitris* were next studied. A highlight was the finding that in this genus there was a very long interval (often up to 2 years) between pollination and fertilization. The comparative studies also enabled her to determine which species were primitive and which were relatively advanced (1953).

Indian botanists working on the embryology of families with representatives in Western Australia, have utilized preserved material of Western Australian plants sent on request. One investigation of particular interest for Western Australian botany dealt with the embryology of Nuytsia floribunda (Narayana 1958).

Cyto-genetics and Genetics

Investigations in the areas of Cytogenetics and Genetics are concerned primarily with understanding genetic mechanisms in the biology of plants which have a bearing on evolutionary processes. In the early 1950s, a frequent visiting scientist at the University of Western Australia, was Dr. Smith-White of the Sydney Botany Department. He was studying the question of the possible lines of evolution in certain pan-

Australian plant families and while here made extensive collecting trips to enable him to make chromosome counts on Western Australian representatives in the families Myrtaceae, Rutaceae and Epacridaceae (1955, 1959). This work with his studies of the eastern States representatives enabled him to conclude that the hardwood genera in Australia were established during the early part of the Tertiary and that differences in chromosome number must have been characteristic of these genera then as now (1959), Two of Smith-White's research students (S. H. James 1965, and B. Barlow 1959) have worked on Western Australian plants. Dr. S. H. James was appointed to the staff of the Botany Department, University of Western Australia in 1963 and with his own research students has continued the genetic evolutionary study of Western Australian plants he began in Sydney. His main published work (James 1963, 1965, 1969, 1970) has dealt with Isotoma petraea which species occurs in small isolated populations inhabiting granite outcrops in the Bullfinch-Laverton area. Between these populations migration and gene exchange are greatly restricted. The species is self-pollinated and in-breeding, and James has been able to show that complex hybridity (or ability to breed true) has evolved in the south-west niche. He suggested that this complex hybridity was maintained by the presence of a balanced lethal system acting at the zygotic level (James 1963, 1965). One of his research students I. C. Beltran (1970) studied embryo-sac formation and the embryogeny of the species and with James has been able to confirm experimentally the presence of a balanced lethal system, the operation of which may be expressed by the abortion of the affected seeds before or after differentiation of the testa has begun (James and Beltran 1970). In attempting an explanation of the development of complex hybridity in Isotoma petraea James (1969) postulated that it probably arose as an adaptive adjustment and was incorporated through natural selection.

Another of James' students (Dr. J. A. McComb, nee J. Chessell) in a study of the evolution of sex has analysed the sex forms in plants of the south-western and south-central Australian flora (1966). Although these two regional floras have been substantially isolated since at least the mid-Tertiary, no significant sex forms differences were found between them. This suggested that following isolation, factors such as climate and soil were not important here. A visiting student from U.S.A. (J. Anway) also working under the direction of Dr. S. H. James studied Calectasia cyanea which extends in distribution from south-western Australia to western Victoria. He noted little variability within the populations, the eastern and western parts of which had been separated since Miocene times. He ascribed the relative lack of variation to the presence of a stabilizing mechanism in the ninth chromosome (Anway 1969).

L. Bousfield (Ph.D. Thesis 1971) of King's Park Botanic Gardens staff, studied under Dr. James the cytogenetics and distribution of Dampiera linearis in the south-west botanical province. He found that the forms occurring on the laterite (a fossil soil developed in the Tertiary) in the Busselton region were diploid while those on younger soils were tetraploid. It appeared that the development of tetraploidy enabled them to colonize these new areas. Hexaploids which were later derived from the tetraploids are now found to be widely distributed in the south-west,

Following Carlquist's suggestion (1969) that adaptations to pollination vectors and soil mosaic patterns were possible factors concerned in the high degree of speciation characteristic of the genus *Stylidium* in Western Australia, Dr. James and his research students (in as yet unpublished work) have found cytogenetic factors (chromosome number variation and lethal systems) also to be involved.

The above examples of cytogenetic research which highlight the evolutionary and taxonomic complexities within a genus or a single species of a genus need to be continued and widened in scope since such work has great potential value for an adequate understanding of the evolution of our flora. In this connection the researches of eastern States botanists who have included the Western Australian representatives of pan-Australian genera in their studies, on evolution, are relevant (cf. Rao 1957, Pryor 1959, Johnson and Briggs 1963, Carr et al. 1971 and Barlow 1971).

The important results from the above cytogenetic researches indicate the pressing need for conservation of vegetation in selected areas. The warning sounded by Williams (1948) for ecological studies and relating to increasing and indiscriminate land use and the risk of fiercer bush-fires, applies even more cogently to cytogenetic studies. If species are placed at risk and face extinction, priceless genetic material could well be lost.

Eco-Physiology

As stressed by Wood (1939) the question of drought resistance is of primary importance to Australia since some four-fifths of its area comes within the 25 cm annual rainfall isohvet. Ecophysiology studies the effects of climate and soil on physiological processes in plants with the aim of throwing light on any apparent physiological adaptations, and of determining whether there is functional significance in any morphological modifications present. Morphological modifications such as sunken stomata, thick cuticle, hairy or waxy leaf coverings, and reduction in leaf area or complete aphylly collectively are described as xeromorphy. Many theories, including an early one that long, continued water stress was a causal agent, have been put forward to explain their origin. The fact, however, that xeromorphy occurs not only in plants growing in dry areas but also in areas not necessarily subject to water stress (as in parts of eastern Australia), has in more recent times downgraded the adaption to aridity theory and led to increasing emphasis being placed on the

soil phosphate mineral deficiency theory (Beadle 1954, 1968). But regardless of the causes which may have brought these xeromorphic modifications into being in the remote past the question still remains whether, when they are present in plants growing in areas subject to severe summer drought, they have any functional significance for survival.

Diels (1906) emphasized that xeromorphic modifications were a conspicuous feature of plants growing in the summer-dry southwestern area of Western Australia. He however did not completely espouse Schimper's view (1898-1903) that such xeromorphic modifications were neccessarily adaptations for reducing transpiration to a minimum. Shelton (1921) became interested in this problem and described the xeromorphic modifications in the leaves of several south-west species. He elaborated on these features and their apparent significance in his presidential address to the Society (1934). On the basis of the morphological features alone, however, hc considered that restriction of water loss was favoured, enabling such plants to survive the succession of long dry summers. Ashby (1933) in considering the overall problem of xeromorphy pointed out, however, that conclusions regarding reduction of transpiration rested on insecure foundations, unless and until they had been tested by experiment. Accepting this viewpoint the writer together with his research students (Holland, Doley, Pearman and Hellmuth) has carried out experimental studies on the field physiology (water relations, photosynthesis, heat resistance and reflectance) of selected native plants. For sclerophylls it was in general found that with increasing summer stress the rate of water loss decreased while osmotic potential and water potential values fell (Grieve 1953, 1955; Grieve and Hellmuth 1970). An important exception was the jarrah (Eucalyptus marginata) which showed some reduction of water loss by mid-summer, but due apparently to its deep-rooting system managed to avoid any severe stress (Doley 1967), Non-native mesomorphs grown under similar conditions in the field, failed to control their water loss and finally showed permanent wilting and died. In native plants of the south-west botanical province, whether scleromorphs or mesomorphs (such as Phyllanthus calycinus), the droughttolerating or drought-avoiding mechanisms noted included stomatal control and progressive defoliation under stress.

Hellmuth (1967, 1968, 1969, 1971) extended the rcsearches into a very dry environment at Cue in the Austin botanical district. He made comparative studies of the field physiology (transpiration, photosynthesis, osmotic quantities and heat rcsistance) of characteristic sclerophyll, semi-succulent and mesomorphic plants. He demonstrated that these plants displayed considerable physiological diversity and that a varicty of adaptations including stomatal control and presence of thick cuticles affecting survival, operated. Pearman (1965) showed that leaves with hairy or waxy covering (which are also a fcature of many plants in south-western

Australia) possessed a high reflectance value. In such plants also he noted that as their water deficits increased so did their leaf reflectance values. These results suggested that those morphologic features and physiologic factors which enhanced reflectance were of ecological advantage to the plant.

The results of the overall eco-physiological experiments so far, suggest that regardless of their original causation the xeromorphic features present do have functional value as adaptations assisting survival under summer stress conditions in south-western Australia. In those cases where external xeromorphic features are lacking and yet the plant survives without defoliation in summer (cf. Hibbertia pungens with marked xeromorphy and H. tcretifolia without, both growing in the same habitat) clearly internal physiological factors operate. What Ashby (1933) described as a possible "tuning" of the protoplasm needs investigation. In this connection it may be noted that Holland (M.Sc. Thesis 1953) showed that for Eucalyptus calophylla (Marri) there was something innate to the plant in drought resistance in terms of resistance to desiccation and in recovery after prolonged wilting, Hellmuth (1969) obtained a similar result for Acacia craspedocarpa. There is obviously still much to be explained here and further studies on such aspects as drought resistance, epharmosis in lcaves, leaf aphylly, root growth and salt and water uptake are desirable for a better understanding of the overall field physiology of native plants. Such studies would have considerable relevance to future decisions on land use for agriculture, forestry and mining.

Plant Physiology.

In considering research which comes within the scope of plant physiology we may note first that basic and highly valuable research directed essentially towards growth and nutrition (including nitrogen, phosphorus and trace element) relations of crop plants has been proceeding for a long time in the State Department of Agriculture, in the Institute of Agriculture at the University and in the Regional Laboratories of C.S.I.R.O. However these researches will not be considered here as they are held to lie outside the scope of this essentially botanically oriented review. Here we shall confine discussion to those plant physiological studies which relate to native plants or which use proven "guinea-pig" indicator plants not considered in any crop context.

Shortly after his appointment in 1914-15 Professor W. Dakin (Biology Department, University of Western Australia) became interested in the biology of the Albany Pitcher Plant (Cephalotus follicularis). He found that the pitchers captured insects in large quantities and that a protease type ferment was present which might facilitate very slow digestion of the insects (Dakin 1919). Further researches which he foreshadowed were not completed owing to his return to England in 1920. Another unique West Australian plant, the Christmas Tree (Nuytsia floribunda) was the subject of a detailed study by Herbert (1919). He was able

to prove that its roots were parasitic upon those of other plants, attachment being by way of collar-like haustorial structures. He also noted the fact that although seed production was high seedling plants were very rare and generally died off young. Those that survived were assumed to have made early connection with a host root. Main (1947) concluded from field observations that non-finding of a host root was not the essential factor causing the death of the young Nuytsia plant; he believed faulty root formation was involved and attempted by the use of root-hormonec to activate sound root growth. Some of his treated seedlings survived and grew successfully without a host for at least a year or so. He considered that further extensive trials would be necessary to clarify the situation.

In 1958 the writer commenced a study of the physiology of *Nuytsia floribunda* with special reference to germination and growth without a host plant. Although the work has not yet been published apart from a brief article in 1963, the following is a summary of results.

Germination in surface sterilized and depericarped seeds remained high (90-100 per cent) for nine months. The usual early death of seedlings could be deferred by up to eighteen months in sand-nutrient-tap water culture. Treatment with a range of growth factor chemicals produced a favourable response. The most effective was gibberellic acid (100 p.p.m.); treated seedlings survived without a host for up to three years.

Following the discovery in 1963 of an unusual case involving production of haustorial collars of Nuytsia roots on underground plastic covered electric cables a study was undertaken by Doley and Grieve. This also is as yet unpublished but the main results are as follows. The formation of the parasitic haustorial collars has been shown to be a response to chemical stimuli and not just a mechanical effect following contact. Nuytsia roots consistently by-passed pieces of wooden dowelling and lengths of rough and polished glass rod, while they vigorously "attacked" lengths of several different kinds of cable. Coverings of butyl rubber, red nylex, nylon, polythene and termite-resistant PVC all had haustorial collars formed around them. In additional experiments it was also observed that Nuytsia roots actively "attacked" plastic flower pot containers, but the haustorial cushions were flat structures. Some evidence was obtained to suggest that ethylene or ethylenic compounds might be the stimulating substances involved in inducing attack by the Nuytsia roots on plastic covered electric cables.

Keeping to the subject of unique Western Australian plants and their physiology mention may also be made at this point of the work of Drs. A. J. and J. A. McComb (University Botany Department) on *Pilostyles hamiltonii*. This plant is completely parasitic upon its hosts (*Daviesia pectinata*, *D. polyphylla* and *D. rhombifolia*), its flowers appearing from protuberances on their stems (Gardner 1948; Smith 1951), Because of its importance in plant geography (see page 12) it appeared desirable to try and learn further details of its life history. With this in mind the above workers carried out experiments designed to induce development apart from its host, in aseptic culture. Results so far have not proved rewarding but the experiments are proceeding.

In this section also we may perhaps mention the work of Lloyd on the mechanism of action of the insect traps in Utricularia. Professor Lloyd spent some time collecting and examining species of Utricularia in our south-west area and was able to extend his findings. He describes the operation of the traps as follows (Lloyd 1936). By glandular action of the walls, water is pumped out from the interior of the trap, so that the walls become concave with the reduced pressure. When the tripping mechanism of projecting stiff bristles on the door surface is activated by a slight touch, as by say a copepod bumping against them, the door opens, the water rushes in, and carries with it the offending animal.

The main area of plant physiology which has developed in Western Australia, in terms of the defined area of comment as set out earlier, relates to growth hormone work. Since his appointment to the University Botany Department in 1963, Dr. A. J. McComb and his research students have concentrated on gibberellin growth hormone physiology.

McComb (1965) first found that gibberellic acid stimulated internode expansion in floating rosettes of the aquatic plant Callitriche stagnalis. Floating shoot parts had been observed in nature to be shorter than submerged shoot parts and the effect of gibberellin was found to be due to its ability to offset the effect of water loss by transpiration in such shoots. In a further anatomical investigation into the effects of gibberellic acid on the expansion of Callitriche shoots, McComb with his research student C. H. Wong, was able to show, using light and electron microscopy techniques, that the greater internode length was due to increase in both cell length and cell number (Wong and McComb 1967). In a study of the effect of gibberellic acid on unvernalized rosettes of *Centaurium* minus held under long day and short day conditions, McComb (1967) observed that only under long day, did stem clongation followed by flowering occur. The results of further experiments suggested that it was only under long day that the production of endogenous gibberellins was stimulated in the flower primordia.

Using intact dwarf pea seedlings McComb (1966) was able to show that the addition of gibberellic acid brought about an increase in the rate of dry weight incorporation into expanding internodes. This themc was then elaborated with one of his research students, the emphasis being on how the gibberellin acted. It was found that gibberellin stimulated protein synthesis and cell wall synthesis and increased the amount of soluble nitrogen in expanding internodes (Broughton and McComb 1967), Broughton (1969) extended the scope of this work to include study of the relations between DNA,

RNA, protein synthesis and the cellular basis of the growth response in gibberellin treated pea internodes. One of the main discoveries was that in treated internodes there was at least a doubling of the total RNA and protein and that the length of the internodes was closely related to the content of these metabolites. Continuing this line of study Broughton and McComb (1970) showed that the overall effect of gibberellic acid on enzymic development was to provide more substrate (particularly glucose) to general cell metabolism and wall synthesis in elongating internodes of Pisum sativum. In a further study Broughton, Hellmuth and Yeung (1970) advanced the hypothesis that gibberellic acid actively directed glucose supply towards elongating internodes.

Another area of enquiry relating to growthhormone physiology was directed towards their implication in the growth of marine algae. Dr. McComb and his student (R. Jennings) made an interesting extension of our knowledge regarding the importance of gibberellins as endogenous growth regulators in a red alga (Hypnea musciformis), in a green alga (Enteromorpha prolifera) and in a brown alga (Ecklonia radiata) (Jennings and McComb 1967; Jennings 1968). In further work by Jennings (1968, 1969, 1970) the presence of cytokinins as endogenous growth regulators in the abovenamed red and brown algae and the presence of a regulatory gibbcrellin antagonist in the brown alga, Ecklonia radiata, were reported. The overall data led him to suggest that growth regulating substances may have arisen early in algal evolution.

An intcresting sidelight on early physiological plant pathologic studies in New South Wales on the fungus Gibberella fujikuroi var subglutinans and its effect on the germination of grain and elongation of internodes in Maize carried out by Edwards (1935) has been provided by McComb and Rizvi (1968). Edwards had suggested that the fungus might produce a growth promoting substance similar to that produced by Gibberella fujikuroi attacking rice as described in the Japanese literaturc. McComb and Rizvi were able to confirm this by isolating gibberellin from cultures of the fungus. As they point out, if Edwards had been able to continue his work the knowledge of gibberellins might well have become widely known outside Japan (publications there commenced in 1926) before its late discovery by the rest of the scientific world in 1951 and consequently the history of thought concerning plant growth control might have been very much altered.

Two other quite different areas where basic plant physiological approaches have been applied by Dr. McComb and his research students may finally be mentioned. The first, verging on ecophysiology, was concerned with the relation between gcrmination requirements and the composition of summer and winter annuals in an arid zone. J. Mott (Ph.D. student) has shown that in the grass *Aristida* contorta which normally germinates after summer rain and sets seed in autumn, dormancy was maintained largely by mcchanical means in the glumes until the following summer. In the case of the composites, *Helipterum craspedioides* and *Helichrysum cassinianum* seeds were produced in spring, remained dormant over summer and germinated with winter rains. The dormancy mechanism here was shown to be an endogenous afterripening effect. Heavy rain in the case of both grasses and composites appeared essential for germination while temperature in the seed bed also played an important part in determining germination once dormancy had been broken.

The second area of investigation centred round the study of the importance of proteoid roots (dense clusters of rootlets produced in many taxa of the family Proteaceae) with particular reference to their occurrence in *Hakea* species. B. Lamont (Ph.D. student) in a projected series of publications has described their morphology and anatomy and the effect of soil nutrients on their production. Proteoid roots have been shown to be produced by the youngest roots in the root system, and to be relatively short-lived surviving for only two to three months. It has also been shown that endophytic organisms are not normally associated with them. In an in-teresting extension of the study it has been demonstrated that proteoid roots also occur on the legume Viminaria denudata. This may allow new insights into whether these structures have any special function.

Concluding remarks

This completes the outline of this review. It is apparent that over the period 1900-1971, during which time many new facets of modern botany developed, there has been a highly significant increase in the extent and depth of our knowledge. This survey has ended at an arbitrary point in time determined by the date of a presidential address. This is not that important. What is important is that the science of botany will keep advancing. While it would be futile to attempt to predict, in terms of Bower's fan-like development concept, which facet or facets of modern botany will be involved in the next big push forward, one may venture to hope that in the future, developing imbalances will be controlled, that some of the more obvious lacks in our botanical knowledge will be remedied, and that current promising lincs of enquiry will be brought to fruition.

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Appendix

History of the development of botanical institutions in Western Australia

In the course of the preceding survey emphasis naturally has been upon developments in botanical research in the different fields. But it may perhaps be helpful to illustrate how the advancement of botany has been related to personnel and establishments.

Dealing first with the official Government appointments it may be noted that the positions of Economic Botanist (Stoward, 1911-17; Her-bert, 1918-21; Praaf, 1921-22; Campbell, 1922-23; Carne, 1923-28), Government Botanist (Gardner, 1929-60) and Officer-in-Charge, Botany Section, and Curator of the Herbarium (Royce, 1960+) were held within the State Department of Agriculture. The State Herbarium has been successively housed in part of the Observatory Building (1933-58), in the Department of Agriculture Laboratories, Jarrah Road, South Perth (1958-69), and finally from March, 1970, in its own new building. Currently a staff of nine professional botanists is engaged on taxonomic and ecological studies. A new journal "Nuytsia" provides for the publication of the results of their researches.

Botany in the University of Western Australia developed in the Biology Department, commencing in 1914. Professor W. Dakin (primarily a zoologist but with an interest in the physiology

of plants as shown by his study of Cephalotus follicularis, the Albany pitcher plant, and his translation of a large part of Diels' "Die Pflan-zenwelt von West Australien") and Dr. Cayzer (taxonomic botanist) comprised the staff. Prowas succeeded by Profesfessor Dakin (zoologist) in 1921 and Dr. sor Nicholls Cayzer by Miss E. Reed about the same time, Towards the end of the 1920s Botany achieved autonomy and moved from the Biology build-ing north of Stirling Highway to a separate building on the main campus at Crawley. Dr. Armstrong succeeded Miss E. Reed as Head of Department in 1930-31 and with Miss A. M. Baird. (who was appointed to the staff in 1934). continued until world war II commenced in 1939. On the outbreak of war Dr. Armstrong joined up and Miss Baird acted as Head of Department from then until 1947 when the influx of exservicemen necessitated expansion of staff. Dr. B. J. Grieve was appointed as Head in 1947 and foundation Professor in 1956.

In 1970 a new Botany building well equipped for studies in descriptive and experimental botany was completed and occupied on Hackett Drive at the southern end of the campus. A small teaching botany garden was developed being laid out to show a possible evolutionary sequence of plant development and incorporating a variety of ecological niches. The professional staff at that time numbered nine and the major facets in Botany were represented by specialists.

In 1959-60, following a report by a Government appointed committee and a further recommendation by Dr. W. Stewart, Director of the Los Angeles State and County Arboretum (who at the time was a Fulbright Scholar in the University Botany Department), a Botanic Gardens essentially for native plants was approved for establishment in King's Park. In 1961 Dr. J. S. Beard was appointed as the first Director. Following four years of development the Botanic Gardens was officially opened in 1965.

Botanists both professional and amateur, through publications in the Royal Society of Western Australia, the Western Australian Naturalists' Club and a variety of specialist Australian and overseas scientific journals, have contributed considerably to the development of botany in this State as outlined in the course of the preceding presidential address.